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SHORT COMMUNICATION

At the northern edge of the Adriatic: First records of the invasive *Caulerpa cylindracea* in the Gulf of Trieste

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Abstract: The non-indigenous green alga *Caulerpa cylindracea* is among the most invasive macroalgae in the Mediterranean Sea and has progressively expanded throughout the Adriatic basin since its first record in 2000. This study reports the first records of *C. cylindracea* in the Gulf of Trieste, the northernmost part of the Adriatic Sea. The species was first recorded in September 2022 at San Bartolomeo (Italy), where only a few thalli were recorded within a *Cymodocea nodosa* meadow. In September 2023, two thalli were recorded at Lazaret, representing the first record of the species along the Slovenian coast. Targeted surveys conducted between 2023 and 2025 documented the current spatial extent of the species at both sites and revealed an additional population at the Rex site, between the towns of Koper and Izola. At San Bartolomeo, *C. cylindracea* occupied an estimated 14,497 m² in July 2023 and 12,331 m² in September 2024. At Lazaret, the species occupied an estimated 12,114 m² by September 2025, while the newly recorded population at the Rex site, between the towns of Koper and Izola, covered approximately 3,000 m². Because the surveyed areas were not monitored systematically before the initial detections, these estimates represent the observed spatial extent of the populations at the time of each survey rather than a quantified rate of spread. These findings confirm the establishment of *C. cylindracea* in the Gulf of Trieste, extend its known distribution to the northernmost part of the Adriatic Sea, and provide a baseline for future monitoring and assessment of its ecological impacts in this environmentally heterogeneous coastal basin.
Keywords: *Caulerpa cylindracea*; biological invasion; Gulf of Trieste; Adriatic Sea; benthic habitats

Sažetak: NA SJEVERNOM RUBU JADRANA: PRVI NALAZI INVAZIVNE VRSTE *CAULERPA CYLINDRACEA* U TRŠĆANSKOM ZALJEVU. Neautohtona zelena alga *Caulerpa cylindracea* jedna je od najinvazivnijih makroalgi u Sredozemnom moru te se od prvog nalaza 2000. godine postupno proširila cijelim jadranskim bazenom. Ovo istraživanje donosi prve nalaze vrste *C. cylindracea* u Tršćanskom zaljevu, na najsjevernijem dijelu jadranskog mora. Vrsta je prvi put zabilježena u rujnu 2022. u San Bartolomeu (Italija), gdje je unutar livade morske cvjetnice *Cymodocea nodosa* pronađeno svega nekoliko talusa. U rujnu 2023. na lokalitetu Lazaret zabilježena su dva talusa, što predstavlja prvi nalaz vrste uz slovensku obalu. Ciljana istraživanja provedena između 2023. i 2025. godine dokumentirala su trenutačnu prostornu rasprostranjenost vrste na oba lokaliteta te otkrila dodatnu populaciju na lokalitetu Rex, između Kopra i Izole. U San Bartolomeu je *C. cylindracea* u srpnju 2023. zauzimala procijenjenu površinu od 14.497 m², a u rujnu 2024. 12.331 m². Na lokalitetu Lazaret vrsta je do rujna 2025. zauzimala procijenjenih 12.114 m², dok je novootkrivena populacija na lokalitetu Rex, između Kopra i Izole, obuhvaćala približno 3.000 m². Budući da istraživana područja prije prvih nalaza nisu bila sustavno praćena, navedene procjene predstavljaju zabilježenu prostornu rasprostranjenost populacija u vrijeme pojedinog istraživanja, a ne kvantificiranu stopu njihova širenja. Ovi rezultati potvrđuju uspostavu vrste *C. cylindracea* u Tršćanskom zaljevu, proširuju njezino poznato područje rasprostranjenosti na najsjeverniji dio Jadranskog mora te predstavljaju polazišnu osnovu za buduće praćenje i procjenu njezinih ekoloških učinaka u ovom okolišno raznolikom obalnom području.
Ključne riječi: *Caulerpa cylindracea*; biološka invazija; Tršćanski zaljev; Jadransko more; bentoska staništa

INTRODUCTION

Marine biological invasions represent one of the major drivers of biodiversity loss and ecosystem alteration in coastal environments worldwide (Simberloff *et al*., 2013; Galanidi *et al*., 2023). In the Mediterranean Sea, non-indigenous macroalgae have shown particularly high invasion success, often forming dense stands that profoundly modify native benthic assemblages and ecosystem functioning (Boudouresque and Verlaque, 2002).

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Among these, the siphonous green alga *Caulerpa cylindracea* Sonder (Chlorophyta, Bryopsidales), previously referred to as *Caulerpa racemosa* var. *cylindracea*, is considered one of the most successful marine invaders in the basin (Klein and Verlaque, 2008).

Caulerpa cylindracea is native to south-western Australia, where it occurs in warm-temperate environments (Verlaque *et al*., 2003). The species was first recorded in the Mediterranean Sea in the early 1990s, with the earliest confirmed observation reported from Libya in 1991 (Nizamuddin, 1991; Bazairi *et al*., 2013). Following its initial detection, *C. cylindracea* spread rapidly throughout the basin, reaching most Mediterranean coastal regions within two decades (Piazzi *et al*., 2005; Klein and Verlaque, 2008). Molecular and morphological evidence indicate that Mediterranean populations belong to a single invasive lineage, distinct from native Australian populations (Verlaque *et al*., 2003; Nuber *et al*., 2007).

The vector of introduction into the Mediterranean remains uncertain (ballast waters, intentional introduction, or accidental escape from aquaria); however, its subsequent large-scale dispersal appears to be primarily driven by natural hydrodynamic processes rather than direct human transport (Verlaque *et al*., 2015; Cantasano *et al*., 2024). This contrasts with other invasive macroalgae, such as *Caulerpa taxifolia* (M.Vahl) C.Agardh, whose long-distance spread has been largely associated with anchoring and fishing activities. In the Adriatic Sea, the distribution of *C. cylindracea* closely follows major current systems, particularly the cyclonic circulation (Žuljević and Antolić, 2005; Iveša *et al*., 2015).

The first record of *C. cylindracea* in the Adriatic Sea dates to autumn 2000, when the species was discovered near Marinkovac, an islet which is part of the Pakleni Islands (central Adriatic Sea), where it formed dense colonies on rocky and sandy substrates between 5 and 15 m depth (Žuljević *et al*., 2003). At the time of discovery, the alga already exhibited high biomass and canopy density, indicating an established population rather than a recent arrival (Žuljević *et al*., 2003).

Following this initial record, *C. cylindracea* rapidly expanded along the eastern Adriatic coasts, with 35 locations documented at the end of 2004, particularly between Cavtat and Vis Island (Žuljević and Antolić, 2005). The species was subsequently recorded along the Albanian and Montenegrin coasts (reported in Žuljević and Antolić, 2005), as well as in the western Adriatic, near Bari (Bello *et al*., 2004) and in the Acquatina Lake (Petrocelli *et al*., 2009).

In the northern Adriatic, *C. cylindracea* was initially considered constrained by lower winter temperatures (Iveša *et al*., 2015). Nevertheless, stable populations were documented in Istria as early as the 2000s, including records near Vrsar, which for several years represented the northernmost confirmed occurrence of the species in the Mediterranean Sea (Iveša and Devescovi, 2006). Subsequent surveys revealed a progressive northward expansion along the western Istrian coast, with numerous new records extending from Vrsar to Zambratija, demonstrating the species' ability to persist and proliferate under comparatively cooler Adriatic conditions (Sladonja and Banovac-Kuča, 2014; Iveša *et al*., 2015). However, despite this progressive expansion, no records had been reported from the Gulf of Trieste, leaving a critical gap in the understanding of the species' northern distribution limit and invasion dynamics in the Adriatic Sea.

The invasion success of *C. cylindracea* is attributed to its high ecological plasticity, allowing colonization of a wide range of substrates, including rocky bottoms, sandy and muddy sediments, and seagrass meadows, from the surface down to depths exceeding 60–70 m (Piazzi *et al*., 2016). The species spreads efficiently through vegetative fragmentation, with stolons and thallus fragments capable of rapid reattachment and growth (Ceccherelli and Piazzi, 2001).

Despite evidence of *C. cylindracea* presence along the central and southern Adriatic coasts, the species had not previously been recorded in the Gulf of Trieste. The present study documents the first record of *C. cylindracea* in this area, representing the northernmost record of the species in the Adriatic Sea. Beyond reporting its presence, we document its current spatial expansion at three sites between 2022 and 2025, characterize the habitats colonized in the lower mediolittoral and infralittoral zone, and discuss the implications of this finding in the context of the ongoing invasion dynamics in the Adriatic Sea. Understanding the early stages of invasion at the expanding distribution edge is critical for predicting future spread and informing management strategies, particularly in environmentally variable systems such as the northern Adriatic. By providing spatially explicit baseline data, this study aims to support future monitoring efforts.

MATERIAL AND METHODS

Study area

The Gulf of Trieste (GoT) is a small, shallow, semi-enclosed basin (~500–550 km²; maximum depth ~25 m) located at the northernmost end of the Adriatic Sea, where physical conditions are strongly shaped by atmospheric forcing and freshwater inputs (Malačič and Petelin, 2001). The hydrography of the GoT is particularly sensitive to the discharge of the Soča/Isonzo River and to episodic strong wind regimes (notably bora and sirocco), which jointly regulate surface circulation, stratification, and short-term variability in temperature and salinity (Malačič *et al*., 2006; Lombardo *et al*., 2025). Tondelli *et al.* (2025) reported a pronounced seasonal cycle in water temperature in Gulf of Trieste based on monthly mean values, with the lowest monthly mean recorded in February (8.93 ± 0.03 °C) and the highest monthly mean in August (23.56 ± 0.05 °C). The same

study also reported a significant positive temperature trend over the 2001–2022 period, ranging from +0.06 to +0.07 °C year^{-1} depending on the site, with an average trend of approximately +0.06 °C year^{-1}. Recent analyses highlight that the interaction between wind stress and river outflow can rapidly reorganize surface currents and coastal transport pathways in the GoT (Lombardo *et al*., 2025), with implications for the dispersal of buoyant or drifting material, including propagules of non-indigenous species (Hansen *et al*., 2024). Additionally, the Gulf of Trieste has been the focus of long-term observational programs and monitoring frameworks that document environmental variability and trophic conditions, thereby providing an important baseline for detecting ecological change in the northern Adriatic Sea (Acquavita *et al*., 2025).

Fieldwork and data analyses

Fieldwork was conducted using non-destructive underwater visual surveys in the infralittoral zone of the Gulf of Trieste. The first observation of *Caulerpa cylindracea* was made incidentally during snorkelling at San Bartolomeo in September 2022. All subsequent surveys were carried out by SCUBA diving within the framework of several independent research projects focusing on coastal benthic habitats and communities. Surveys combined 100-m transects laid perpendicular to the coastline with random area searches to detect and delimit the occurrence of the species.

During these *in situ* visual assessments, *C. cylindracea* (Fig. 1) was recorded at three sites between 2022 and 2025 (Fig. 2). GPS coordinates were collected for the boundaries of the surveyed areas and all confirmed occurrences of the species. The boundaries of each surveyed area were delineated by recording the coordinates of their vertices from the survey boat. To estimate the spatial extent of *C. cylindracea*, the shallowest and deepest occurrence recorded along each transect were georeferenced and used as polygon vertices, together with additional georeferenced occurrence points obtained during random area surveys. Spatial data were processed in QGIS, where occurrence points were converted into lines and subsequently into polygons using the Processing Toolbox to estimate the area occupied by the species. Photographic documentation of *C. cylindracea* and the associated habitats was collected during each survey. Approximately ten representative thalli *per* site and survey year were selectively sampled for morphological identification following Verlaque *et al.* (2015). No reproductive (sexual) structures were observed. Targeted surveys conducted in July 2023, September 2024 and September 2025 were used to assess the spatial extent of the established populations using the same survey protocol.

Thallus abundance was estimated in the field using a semi-quantitative visual scale based on the frequency of thalli (erect fronds). Two categories were distinguished: low, corresponding to scattered thalli with isolated erect fronds and no continuous cover, and medium, corresponding to frequent thalli with several erect fronds and partial but discontinuous cover. These categories represent descriptive field estimates rather than quantitative measures of population density.

RESULTS AND DISCUSSION

Within the GoT, *Caulerpa cylindracea* was first recorded in September 2022 on the Italian side, at the San Bartolomeo site (Ca_cy_1 in Fig. 1). Only a few thalli were incidentally observed at a depth of 0.5 m, within a *Cymodocea nodosa* (Ucria) Ascherson meadow. The site, located near a small marina, is characterised by very fine pelitic sediments. During a follow-up survey in July 2023, the species was found to have expanded extensively throughout the *C. nodosa* meadow, occupying an estimated area of 14,497 m². A subsequent winter survey in February 2024, covering 13,934 m², did not detect any thalli. However, a subsequent survey in September 2024 estimated that *C. cylindracea* occupied 12,331 m² within the same meadow. In both positive surveys, *C. cylindracea* generally occurred at low abundance, with locally medium abundance in the first metre of depth (Table 1, Fig. 2).

On the Slovenian side of the GoT, *C. cylindracea* was first recorded in September 2023 at Lazaret (Ca_cy_2 in Fig. 2.), where two small thalli were detected on rocky substrate at approximately 0.7 m depth within a surveyed area of 12,600 m^2. This site is characterised by sandstone bedrock in the shallowest zone (approximately the first metre of depth), gradually transitioning with increasing depth into a sandy–muddy bottom colonised by *C. nodosa*, which extends down to approximately 7 m depth. During the September 2025 survey, *C. cy-*

Fig. 1. Thalli of *Caulerpa cylindracea* found at site Ca_cy_3 at a depth of 6 m on 19 September 2025. (Photo: Borut Mavrič).

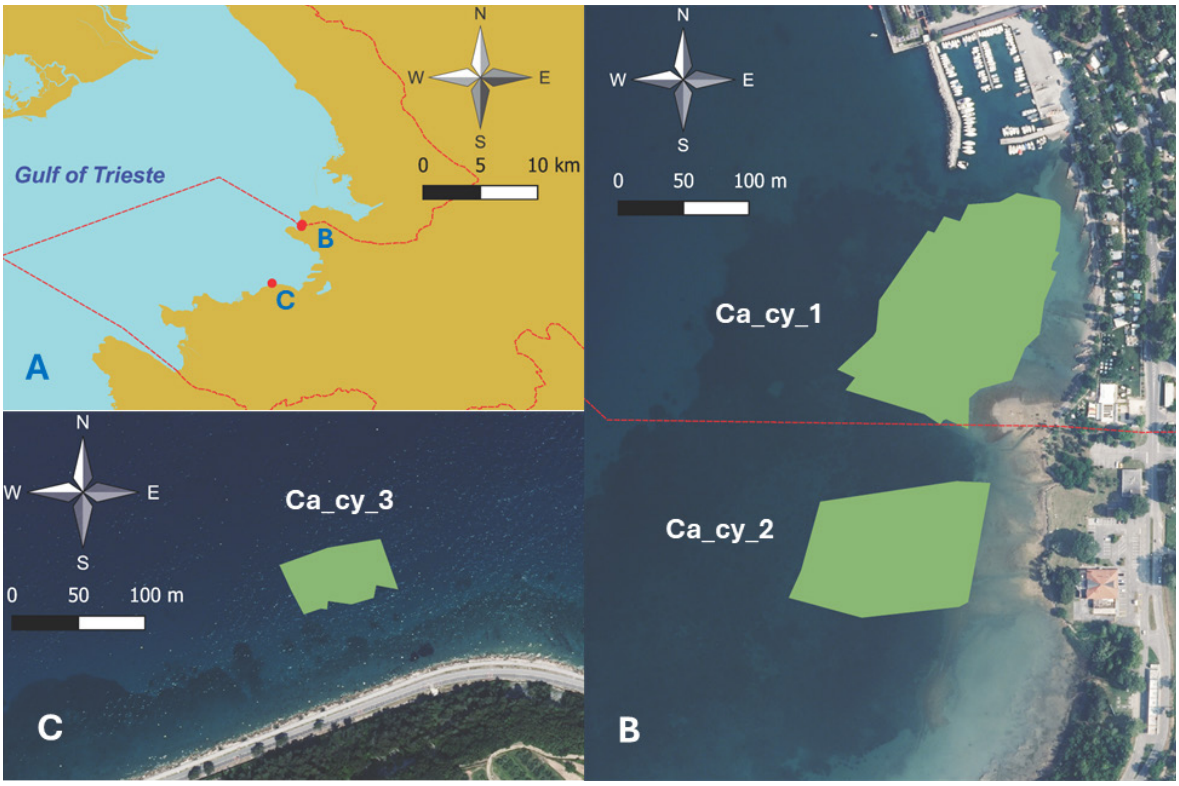

Fig. 2. Distribution map of *Caulerpa cylindracea* in the Gulf of Trieste: general map of investigated area **(A)**; distribution of *C. cylindracea* in 2024 at site Ca_cy_1 (San Bartolomeo, Italy), and in 2025 at sites Ca_cy_2 (Lazaret) **(B)**; distribution of *C. cylindracea* between Koper and Izola (Rex wreck) in 2025 (Ca_cy_3) **(C)**. The border between Italy and Slovenia is indicated with a red line.

lindracea had expanded markedly into the adjacent *C. nodosa* meadow, occupying an estimated area of 12,114 m². Based on expert visual assessment, abundance was highest between 1 and 2 m depth (medium abundance) and gradually decreased with increasing depth. The lower depth limit of occurrence was recorded at 2.9 m (Table 1, Fig. 2).

An additional population of *C. cylindracea* was recorded in September 2025 at the Rex site (Ca_cy_3 in Fig. 2) located between the towns of Koper and Izola. The species occupied an estimated area of approximately 3,000 m² on muddy bottoms between 6 and 8 m depth (Table 1). The thalli were heavily coated with fine sediment and occurred among sparse shoots of *Zostera noltei* Hornemann. No thalli were detected in areas shallower than 6 m. Overall abundance at this site was assessed as medium based on visual field observations.

The present study documents the first records of *Caulerpa cylindracea* in the Gulf of Trieste, representing the northernmost occurrence of this species in the Adriatic Sea and the northernmost record of this species worldwide. This finding extends the known distribution range beyond previously reported northern Adriatic localities along the western Istrian coast, such as Vrsar and Zambratija, which for more than a decade were considered the northern limit of extent (Žuljević and Antolić, 2005; Iveša and Devescovi, 2006; Sladonja and Banovac-Kuča, 2014). In addition to confirming its presence, our results provide the first spatially explicit estimates of the area occupied by *C. cylindracea* in the Gulf of Trieste. Because no systematic survey of the same area was conducted prior to or at the time of the first detection, the mapped coverage observed in 2024 and 2025 should be interpreted as documentation of the species' currently observed spatial extent.

The absence of visible thalli of *C. cylindracea* in February 2024 at Ca_cy_1 (Fig. 1) contrasts with its subsequent presence and mapped coverage in September 2024. Similar reductions in winter biomass followed by renewed growth during warmer periods have been reported for northern Adriatic populations of *C. cylindracea* (Iveša and Devescovi, 2006; Iveša *et al*., 2015). However, because the present study was not based on continuous seasonal or monthly monitoring, this single winter observation cannot be used to confirm seasonal regression or to establish a relationship between presence of thalli and seawater temperature. The observation should therefore be interpreted only as a temporary absence of visible aboveground biomass at the time of survey. Further standardized monitoring across seasons, combined with *in situ* temperature measurements, would be required to evaluate seasonal dynamics, overwintering capacity, and possible relationships with thermal variability in the Gulf of Trieste.

The arrival of *C. cylindracea* in the GoT is most plausibly explained by vegetative dispersal. Fragmentation of

Table 1. Records of *Caulerpa cylindracea* in the Gulf of Trieste, including survey date, inspected area, habitat type, occupied depth range, estimated area colonised by the species, geographic coordinates of the recorded population, and semi-quantitative estimates of thallus abundance based on expert visual assessment. Thallus abundance was assessed in the field using a semi-quantitative visual scale, as quantitative counts of thalli or erect fronds were not performed. Low abundance indicates scattered thalli with isolated erect fronds and no continuous cover, whereas medium abundance indicates frequent thalli with several erect fronds and partial, but discontinuous, cover.

Site	Site name	Survey date	Inspected area (m^2)	Habitat type	Depth range of covered area (m)	Estimated occupied area by *C. cylindracea* (m^2)	Latitude (N)	Longitude (E)	Estimated abundance of thalli (visual assessment)
Ca_cy_1	San Bartolomeo	14.09.2022	incidental observation	*C. nodosa* meadow	0.5	0.002	45°35'43.74"	13°33'24.00"	few thalli
Ca_cy_1	San Bartolomeo	13.07.2023	129,381	*C. nodosa* meadow	0.5-4.0	14,497	45°35'43.74"	13°33'24.00"	low (medium in the first metre depth)
Ca_cy_1	San Bartolomeo	13.02.2024	13,934	*C. nodosa* meadow	0.5-6.0	0	45°35'43.74"	13°33'24.00"	no visible presence
Ca_cy_1	San Bartolomeo	4.09.2024	12,947	*C. nodosa* meadow	0.5-4.0	12,331	45°35'43.74"	13°33'24.00"	low (medium in the first metre depth)
Ca_cy_2	Lazaret	8.09.2023	12,600	rocky substrata	0.7	0.02	45°35'37.80"	13°43'17.64"	only two thalli
Ca_cy_2	Lazaret	3.09.2025	cca 25,000	*C. nodosa* meadow	1.0-2.9	12,114	45°32'55.68"	13°41'22.98"	low (medium in the first metre depth)
Ca_cy_3	Rex	19.09.2025	cca 10,000	muddy bottom	6.0-8.0	cca 3,000	45°35'43.74"	13°33'24.00"	medium

stolons and thalli, followed by transport *via* prevailing currents, represents the dominant dispersal mechanism (Žuljević and Antolić, 2005; Klein and Verlaque, 2008). Sexual reproduction has not been (yet) documented in the Adriatic Sea, with long-term observations reporting exclusively female gamete production (Žuljević *et al*., 2012). The general cyclonic circulation of the Adriatic, combined with regional current systems and episodic bora and sirocco wind events, likely facilitates northward transport of viable fragments from established populations along the Istrian coast (Iveša *et al*., 2015).

The establishment of *C. cylindracea* within seagrass meadows is ecologically significant, even though its cover in the present study was estimated as medium rather than dense. Seagrass habitats play a key role in sediment stabilization, nutrient cycling, and nursery functions (Orlando-Bonaca *et al*., 2015). In our surveys, medium-density *C. cylindracea* was characterized by frequent thalli with several upright fronds and discontinuous cover, indicating that the species is already established within the meadow but has not (yet) formed continuous mats. Although *C. cylindracea* is capable of colonizing a wide range of substrates, its presence within seagrass systems may still represent an early stage of habitat modification, with potential consequences for sediment dynamics and associated benthic communities. Previous studies have shown that dense *C. cylindracea* canopies can strongly alter invaded habitats by trapping sediments and organic matter beneath multilayered mats (Klein and Verlaque, 2008; Matijević *et al*., 2013). While such dense mats were not observed in the present study, the medium-density occurrence recorded here suggests the need for continued monitoring, as further expansion could lead to physical and biogeochemical changes similar to those reported from more heavily invaded habitats. These changes have been associated with reduced diversity and abundance of native macroalgal assemblages and changes in beta diversity (Piazzi *et al*., 2001; Piazzi and Balata, 2008). On rocky substrata the alga can homogenize benthic communities and modify macrozoobenthic assemblages, influencing both species composition and functional diversity (Vázquez-Luis *et al*., 2008; Baldacconi and Corriero, 2009; Mannino and Balistreri, 2019; Sinopoli *et al*., 2020).

In the Adriatic Sea, severe impacts of *C. cylindracea* have been documented on structurally and ecologically important benthic organisms. *C. cylindracea* has been shown to overgrow and smother colonies of the scleractinian coral *Cladocora caespitosa*, causing tissue necrosis and potentially compromising long-term coral bank persistence (Kružić *et al*., 2008). Similarly, dense mats of *C. cylindracea* are reported to negatively affect the epiphytic assemblage of *Posidonia oceanica* rhizomes (Antolić *et al.*, 2008) and are also able to overgrow photophilic sponges such as *Sarcotragus spinosulus*, leading to reduced seawater circulation, anoxia, and sponge mortality (Žuljević *et al*., 2011). Although ecological impacts were not quantified in the present study, and the observed populations were not of high density, the documented coverage exceeding 27,000 m² at three sites indicates that *C. cylindracea* is already spatially established in this anthropogenically influenced basin. These findings highlight the need for density-based monitoring and comparison with heavily invaded sites, where dense mats have been associated with stronger ecological impacts.

The larger occupied areas documented during the 2024 and 2025 surveys indicate that *C. cylindracea* is currently established over relatively extensive areas in the GoT. However, because the surveyed areas were not monitored systematically before the first records, the rate of spread cannot be quantified with certainty. Importantly, this study provides a quantitative baseline for future monitoring. The mapped distribution areas from 2024 and 2025 will allow future assessments of expansion, contraction, or stabilization trends. Early-stage documentation is particularly valuable, as management options become increasingly limited once dense and continuous mats are formed (Klein and Verlaque, 2008).

Overall, the records from the Gulf of Trieste represent the continuation of a long-term northward expansion of *C. cylindracea* in the Adriatic Sea. The combination of hydrodynamic connectivity and ecological plasticity likely facilitates further persistence and spread. Continued, systematic monitoring of northern Adriatic benthic habitats is therefore essential to assess future distribution patterns and potential ecological consequences of this alga.

CONCLUSIONS

The present study reports the first documented records of *Caulerpa cylindracea* in the GoT and provides the first spatially explicit estimates of the area occupied by the species at multiple sites. The recorded occurrences indicate that the species is able to persist locally under the environmental conditions of the northern Adriatic, although the rate of spread cannot be determined without systematic monitoring of the same areas over time. These findings provide the first spatially explicit baseline for this region and will enable future assessments of distribution dynamics, including potential expansion, contraction, or stabilization. Given the documented impacts of *C. cylindracea* elsewhere in the Adriatic, its continued presence in the GoT may have implications for benthic habitats. Sustained and standardized monitoring of coastal benthic ecosystems in the northern Adriatic is therefore essential. Early detection and coordinated regional reporting remain key elements for tracking distributional changes and supporting evidence-based management responses.

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AUTHOR CONTRIBUTIONS

Martina Orlando-Bonaca: Conceptualization; Writing – original draft; Data curation; Writing – review & editing. Lovrenc Lipej: Investigation; Data curation; Writing – review & editing. Borut Mavrič: Investigation; Data curation; Formal analysis; Writing – review & editing. Domen Trkov: Investigation; Data curation; Formal analysis; Writing – review & editing. Neža Leban: Investigation; Writing – review & editing. Leon Lojze Zamuda: Investigation. Annalisa Falace: Data curation; Writing – review & editing. Andrea Gergic: Investigation. Marco Segarich: Investigation. Edoardo Batistini: Investigation. Paola Nichetto: Investigation. Eva Godini: Investigation. Saul Ciriaco: Investigation; Data curation; Formal analysis; Writing – review & editing.

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